



The effects of predation risk on female silk deposition and male response to predator-cued conspecifics in the wolf spider, *Pardosa milvina* (Araneae: Lycosidae)

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Abstract. Female *Pardosa milvina* (Hentz 1844) wolf spiders advertise sexual receptivity toward males via silk draglines, and male *P. milvina* exhibit conspicuous courtship behavior when encountering silk from females. Previous studies suggest that female *P. milvina* may benefit by limiting silk advertisements and excreta deposition when encountering silk from the predator, *H. helluo*, and male *P. milvina* may exhibit corresponding reductions in courtship when encountering silk from conspecific females previously exposed to *H. helluo* silk. We tested these predictions by comparing the amount of silk and excreta deposited by unmated female *P. milvina* exposed or not exposed to predator cues (silk and excreta) from *H. helluo*. We also measured and compared male *P. milvina* courtship latency and intensity in the presence of silk from females previously exposed or not exposed to predator silk from *H. helluo*. Contrary to predictions, we found a significant increase in excreta, dragline, and attachment disk deposition after females were exposed to *H. helluo* cues. Male *P. milvina* courtship latency did not vary among treatments despite increases in female silk deposition, but males significantly decreased courtship intensity when exposed to silk from females under predation risk. Vertical climbing to escape the predator cues may cause an increase in female silk deposition.

Keywords: Dragline, kairomone, pheromone, chemical cue, courtship

Conspicuous ornamentation and courtship displays of male wolf spiders increase mating success by attracting females and provide information about species identity (Stratton & Uetz 1986; McClintock & Uetz 1996; Scheffer et al. 1996; Parri et al. 1997; Hebets & Uetz 1999, 2000). However, elaborate ornaments and complex displays may incur considerable fitness-related costs because of their potential to draw the attention of nearby predators (Kotiaho et al. 1998; Pruden & Uetz 2004; Roberts et al. 2007; Hoefler et al. 2008). Consequently, males may benefit by reducing their overall activity level, including courtship intensity and duration, when under predation risk (Kotiaho et al. 1998; Taylor et al. 2005; Hoefler et al. 2008).

Female wolf spider dragline silk is an important medium for sexual communication (Kaston 1936; Hegdekar & Dondale 1969; Richter et al. 1971; Dondale & Hegdekar 1973; Tietjen 1979; Hebets & Uetz 1999; Rypstra et al. 2003; Schultz 2004; Gaskett 2007) and often serves as an advertisement to males. Although the predation costs associated with conspicuous male displays have been studied in a number of wolf spider species (Kotiaho 1998; Hebets 2005; Roberts et al. 2007; Hoefler et al. 2008), what remains less appreciated is that female silk may be chemically conspicuous to predators and increase predation risk as well, particularly among predators that use silk as a mode of communication. Consequently, females may benefit by reducing or modifying their silk advertisements toward males when aware of the presence of a predator.

A number of studies demonstrate that the wolf spider *Pardosa milvina* (Hentz 1844) can detect fine differences in predation risk through silk and excreta cues left by the larger

predatory wolf spider, *Hogna helluo* (Walckenaer 1837), and respond with graded reductions in activity proportional to the perceived risk. *Pardosa milvina* can determine how recently *H. helluo* was in the area (Barnes et al. 2002), its diet (Persons et al. 2001), its hunger level (Bell et al. 2006), and the quantity of silk and excreta present (Persons & Rypstra 2001). Such discriminatory facilities suggest that *P. milvina* has sophisticated chemoreceptive abilities and that there is strong selection for recognition and evaluation of varying levels of predation risk.

Female *Pardosa milvina* exposed to *H. helluo* silk and excreta reduce activity (Persons & Rypstra 2001) and increase vertical orientation and climbing behavior (Persons et al. 2002; Folz et al. 2006). Exposure to these same cues can change foraging patterns to such an extreme that it directly affects body condition, prey capture behavior, and egg sac production of females, ultimately affecting the direct fitness of the spider (Persons et al. 2002). When in the presence of conspecific adult females, male *P. milvina* respond to *H. helluo* cues by delaying courtship (Taylor et al. 2005). In addition, *H. helluo* is attracted to silk and excreta produced by female *P. milvina* when they have been fed a diet of *P. milvina* (Persons & Rypstra 2000).

Given the potential predation costs associated with female silk advertisements, we addressed two questions: 1) Do female *P. milvina* alter the quantity and type of silk they deposit while in the presence of silk cues from the predatory wolf spider, *H. helluo*?; 2) Do male *P. milvina* respond differently to silk cues from female *P. milvina* that were under predation risk, without being exposed to the predator cues themselves? We predicted that female *P. milvina* would reduce their silk deposition or possibly pheromones associated with the silk when detecting chemical cues produced from the predator, *H. helluo*. If females reduce chemical advertisements toward males when

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under predation risk, then males should also show corresponding reductions in courtship behavior when detecting female silk deposited while the female was detecting a predator in the area, even when the male has no direct access to the predator's cues.

METHODS

Spider collection.—Subadult female *H. helluo* and *P. milvina* were collected in agricultural fields near the campus of Susquehanna University, Selingsgrove, Pennsylvania, Snyder County, USA. To assure the virginity of test spiders, we allowed all spiders to mature in the laboratory. The *P. milvina* were maintained in 0.074 l translucent containers (8 cm diameter, 5 cm height) and *H. helluo* were maintained in 0.473 l (9.8 cm diameter, 8.5 cm height) plastic deli dishes. Each spider was given water ad libitum and fed a diet of juvenile (ca 0.25 cm) domestic house crickets (*Acheta domesticus* Linnaeus) for *P. milvina*, and adult house crickets for *H. helluo*. All spiders were fed 2–3 crickets every 3–4 days, and then fed to satiety 1–2 h before testing to minimize the effects of body condition and hunger level on silk production and male courtship. We only used spiders that had finished feeding at the time of testing.

General experimental protocol.—We collected data relevant to each question with a separate protocol and a different set of males and females. Males in the second protocol and females in both protocols were tested twice, once under conditions of predation risk and once under conditions of no predation risk. We randomized the order of exposure such that half of the test spiders were subjected to the predation risk treatment first while the other half were exposed to the “no predator cue” treatment first. This was done to minimize any confounding effect of experience or other associated sequence effect. We analyzed female silk and male courtship behavior using paired *t*-tests, with predator risk and no risk as independent variables. We conducted tests in September–December, 2006.

Quantifying silk deposition.—We randomly chose 30 adult, laboratory-reared, virgin female *H. helluo* and used them in both parts of the experiment to deposit predator cues for multiple treatments. We placed each female *H. helluo* in a clean, 0.473 l white plastic testing container (9.8 cm diameter, 8.5 cm height) for four hours on a black paper substrate (9.8 cm diameter) printed with a grid to allow us to quantify silk production. Each substrate was divided into a grid of 3 mm \times 3 mm sub-squares (approximately 766 squares). In a second control treatment, we used no predator stimulus in the container but the container setup was otherwise identical. Once the *H. helluo* was removed, we examined each paper substrate for the presence and amount of silk under a dissecting stereomicroscope. Silk types included attachment disks, which were discrete butterfly or u-shaped strands of silk produced by the piriform glands, and thin linear dragline silk produced by the ampullate silk glands (Richter et al. 1971). Each grid sub-square was then scored from 0–4 based on the percentage of the area covered by silk (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%). We also counted the total number of drops of excreta and attachment disks across the entire grid surface. *Hogna helluo* silk served as a predator stimulus for female *P. milvina*. We quantified *H. helluo* silk and excreta prior to the introduction of the female *P. milvina*

in order to calculate the amount of *P. milvina* dragline silk, excreta, and attachment disks. For control trials, we quantified *P. milvina* dragline silk, excreta, and attachment disks alone, with no predator stimulus.

After each grid was scored, we placed a laboratory-reared, virgin, female *P. milvina* in the container for four hours to deposit cues on top of the *H. helluo* silk and excreta or on the blank substrate in control trials. *Hogna helluo* cues were scored within one–two hours of deposition before a female *P. milvina* was placed on the cues. After scoring the first two sets of 15 replicates per treatment ($n = 30$), we reversed the treatments and ran them a second time. After running female *P. milvina*, we scored the grids a second time, subtracting the initial *H. helluo* silk score to estimate female *P. milvina* silk deposition.

Quantifying male *Pardosa milvina* courtship behavior.—To measure the effects of the context in which female silk was deposited on male courtship behavior, it was necessary to separate the cues of the predator *H. helluo* from those of the female *P. milvina* exposed to the predator cues (Fig. 1 A, B). In a clean, 0.473 l container, we placed a single adult, laboratory-reared, virgin female *H. helluo* on a blank white paper substrate for four hours to deposit cues. We then removed the female *H. helluo*, and inserted another 0.473 l dish with the bottom completely removed (a circle of 8 cm diameter), save for an approximately 9 mm rim around the bottom, into the original container. We placed an unmated laboratory-reared adult female *P. milvina* on the substrate in the presence of predator cues with the inserted dish for four hours. No food or water was provided during this time period. We then removed the inserted dish and wiped the bottom with a small amount of ethanol to deactivate and remove any remaining predator cues. After the ethanol had evaporated, we placed the insert in a clean dish with a male *P. milvina* and documented courtship behavior for 30 minutes while the male was exposed to only the female conspecific cues on the 9 mm rim. We ran an identical treatment without the initial presence of *H. helluo* cues (Fig. 1 B). In both treatments, the male was responding solely to the conspecific female silk. As in the protocol for females, both treatments were conducted with the same set of 24 male subjects, assigned randomly to first experience cues from either females with or females without exposure to a predator. We used paired *t*-tests to compare female silk deposition with and without predator cues. We also used paired *t*-tests to compare male courtship latency and courtship intensity across treatments.

We defined courtship in *P. milvina* as a combination of two separate and distinct behaviors, leg raises and body shakes. A leg raise is raising the first pair of legs in unison above the cephalothorax and bringing them down abruptly. A body shake is a set of rapid oscillations of the abdomen and cephalothorax, often in conjunction with a leg raise. These behaviors have been described elsewhere and are known to influence female mate choice (Montgomery 1903; Kaston 1936; Brautigam & Persons 2003). Courtship latency constitutes the time elapsed between when a male was first placed on the substrate and when he began courtship (either with a leg raise or a body shake). We measured courtship intensity as the sum of body shakes and leg raises divided by courtship duration.

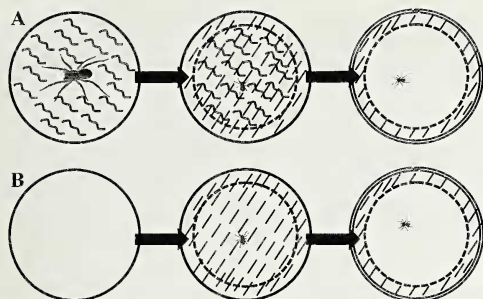


Figure 1.—Experimental containers for measuring behavioral response in male *P. milvina* with (A) and without (B) *H. helluo* silk present during female *P. milvina* silk deposition. A. An adult female *H. helluo* is allowed to deposit silk and excreta on the bottom of a container for 4 hours. A second clean container with the bottom removed (except for a shallow lip along the edge) is nested within the predator-cued container. A single unmated female is then allowed to deposit silk for four hours on top of the predator cues within these two nested containers. The inner container is then removed, the bottom cleaned, and nested into a clean container devoid of predator silk. A single male *P. milvina* is then introduced into the container and its courtship behavior is quantified. Note that males have access only to silk that females deposited while they detected *H. helluo* chemical cues, but that the males have no silk cues available from *H. helluo* directly. B. The same procedure as in A is followed, except female *P. milvina* do not perceive predator cues during silk deposition.

RESULTS

We found that when exposed to cues (silk and excreta) from the larger predatory wolf spider *Hogna helluo*, female *Pardosa milvina* showed a significant increase in deposition of both silk and excreta. When we exposed male *P. milvina* to conspecific cues from females exposed to predator cues, we found that males significantly decreased courtship behaviors and courted significantly less intensely.

Effects of predator cues on female silk deposition.—There was a large increase in total dragline silk (paired $t = 2.449$, $P = 0.0206$), attachment disks (paired $t = 2.708$, $P = 0.0112$) and excreta (paired $t = 2.574$, $P = 0.0154$) from female *P. milvina* when exposed to *H. helluo* cues (Fig. 2 A–C).

Effects of predator-cued female silk on male courtship behavior.—There were significant decreases in male courtship behaviors when exposed to predator-cued, conspecific females. During courtship, males dramatically decreased the total number of body shakes, the intensity of leg raises and the intensity of body shakes when exposed to cues from females under predation risk (Table 1 for all behaviors). Total courtship intensity (leg raises and body shakes/courtship duration) also decreased among males exposed to predator-cued conspecifics (Table 1). Total leg raises showed a qualitatively similar decrease, but the decrease was not statistically significant (Table 1).

DISCUSSION

Our results clearly show that female *P. milvina* produce greater quantities of silk, excreta and attachment disks in the presence of predator cues from *H. helluo* and that in some

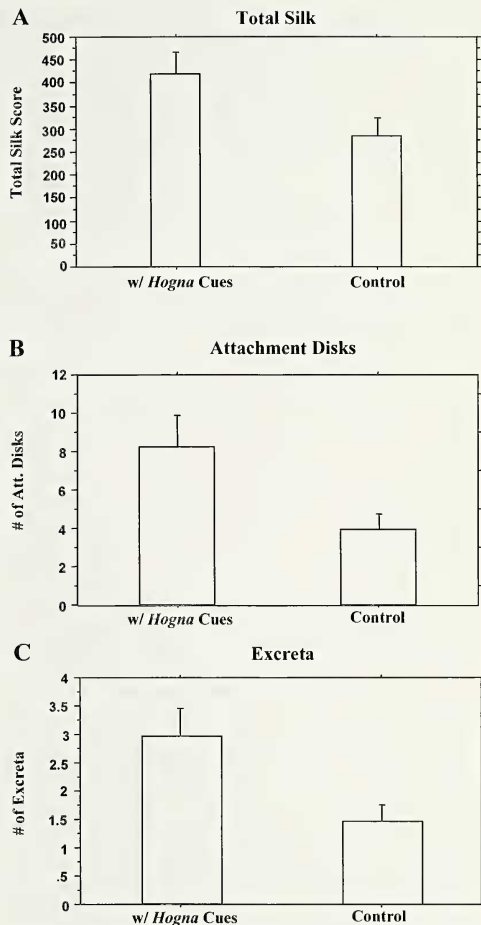


Figure 2.—Female *Pardosa milvina* silk and excreta deposition with and without silk from a predator present. A. Total silk score was calculated as the cumulative sum of all the sub-squares of each grid. Each grid square was scored from 0–4 based on an approximate percentage of the area of the square that was covered by silk. The total possible score if all grid squares were completely covered with silk would be 3064 (see text for more details). B. Deposition of female *P. milvina* attachment disks and C. Excreta. Unlike with the scoring method for total silk, each drop of excreta and attachment disk were discrete and were therefore counted directly.

manner, a potential predator can indirectly affect the behavior of a male even though the male has no direct access to predator cues. Several studies have examined the effects of conspicuous courtship displays of wolf spiders on the probability of attacks from nearby predators (Kotiaho et al. 1998; Pruden & Uetz, 2004; Roberts et al. 2007), but to our

Table 1.—Measures of male courtship behavior (mean \pm S.E.) in response to female silk deposited while the female was exposed to *H. helluo* silk and excreta or control treatments without *H. helluo* cues. *P*-values are based on paired *t* tests. See text for definitions of courtship behaviors.

Behavior	Treatment		<i>t</i>	<i>P</i>
	w/ <i>Hogna</i> cues	Control		
Leg raise number	21.33 \pm 5.2250	46.79 \pm 15.005	1.917	0.0677
Body shake number	2.54 \pm 0.8470	12.08 \pm 4.125	2.718	0.0123
Leg raise intensity	0.0123 \pm 0.0030	0.0279 \pm 0.008	2.135	0.0436
Body shake intensity	0.00148 \pm 0.0005	0.00699 \pm 0.002	2.770	0.0109
Total courtship intensity	0.0137 \pm 0.0030	0.0349 \pm 0.011	2.318	0.0297

knowledge, this is the first study documenting that male courtship behavior can be modified in direct response to the predation context of female silk deposition.

Female silk deposition increased while under predation risk, yet male courtship intensity significantly decreased when encountering silk from a conspecific female that had previously detected predator silk. This surprising result runs counter to several of our predictions. When adult *H. helluo* have been reared on a diet of *P. milvina*, they preferentially choose to forage in areas where adult female *P. milvina* silk and excreta cues are present (Persons & Rypstra 2000). This suggests that females that deposit greater quantities of silk may attract *H. helluo*. If a female is under perceived predation risk, then it may be adaptive to limit the amount of silk deposited to reduce attracting predatory wolf spiders. We might then expect that reductions in silk would lead to an impaired ability of males to detect females, which would translate into increased courtship latency and less intense courtship. However, our results showed that females significantly increased total silk deposited, attachment disks, as well as excreta when under perceived predation risk.

The females that were exposed to a potential predator's cues could be engaging in a number of different anti-predator tactics. Female *P. milvina* increase climbing behavior and attempt to move up the side of a container when the horizontal substrate contains silk and excreta from *H. helluo* (Persons et al. 2002; Folz et al. 2006). This behavior would likely require a greater number of attachment disks as a means of anchoring the spider while climbing. If so, climbing females may release significantly more silk in an effort to escape the container. Alternatively, increased deposition of silk may simply be a non-adaptive reflexive response to an acute stressor such as the presence of predator cues.

Excretion increased in the presence of predator silk as well. Excretion in the presence of a predation threat is known to be an effective anti-predator response for a number of arthropods by either increasing locomotor efficiency or repelling potential predators (Weiss 2006). It is possible that *H. helluo* silk caused *P. milvina* to avoid the center of the container, resulting in proportionally more time spent exhibiting thigmotaxis (wall-hugging). We suggest this is unlikely, however, since numerous studies have shown that female *P. milvina* spend significantly more time on *H. helluo*-cued substrates due to freezing responses. Anecdotal observations of spider dragline deposition suggest that deposition rate is a function of time spent moving. Given that numerous studies have shown that female *P. milvina* locomotion decreases in the presence of *H. helluo*

cues (e.g., Persons et al. 2001; Persons & Rypstra 2001), it suggests that the deposition rate must dramatically increase as a proportion of time spent moving.

The fact that adult males reduced courtship when detecting larger quantities of female silk suggests that there is not a simple positive relationship between the quantity of female silk and male courtship intensity. If anything, our results indicate a negative relationship between these variables. The relative importance of the tactile component of silk versus sex pheromones perfused on silk remains unknown. At least some wolf spider species respond to silk cues that are devoid of pheromones (Tietjen 1977; Tietjen & Rovner 1982), while other wolf spiders, such as *P. milvina*, are able to produce airborne pheromones that induce responses in males independent of male contact with silk (Searcy et al. 1999). Our results suggest that females could have reduced sex pheromone deposition on the silk even while increasing the amount of silk. If *H. helluo* attraction to female *P. milvina* is based on these pheromones rather than silk, increased silk deposition would have little consequence in attracting *H. helluo*. Also, the strength of *H. helluo* preference for cues associated with *P. milvina* may not necessarily be dependent on the quantity of *P. milvina* silk or excreta, but only on the presence or absence of these cues.

Regardless of the proximate cue used to elicit courtship behavior in males, our study provides indirect evidence that qualitative differences in the silk may be more important than quantitative differences in mediating male courtship displays. *Pardosa milvina* appears to produce at least two discrete types of dragline silk, heavy gauge cord silk and fine gauge dragline silk, which has a diameter approximately ten times smaller than heavy gauge silk. The ratio or quantity of these two silk types could vary markedly with and without predator cues, and each silk type may convey different information to males.

One hypothesis that could explain the significant decrease in several male courtship behaviors is that there is a change in the cues deposited among the females when under predation risk. Regardless of the specific source of the female stimulus, males appear capable of appropriately reducing courtship levels which, in turn, likely decreases the probability of predation. Since we know almost nothing about the quantitative relationship between sex pheromone production and silk production in lycosids, this explanation must remain speculative. However, given the sophisticated ability of *P. milvina* to extract a variety of information about predators from silk and excreta cues alone, we believe their chemoreceptive capabilities may be sufficiently advanced that an indirect transfer of

information about the presence of a predator is possible through conspecific female *P. milvina*. Additional studies that examine differences in predation risk based on the quantity of female silk deposited may prove fruitful.

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